Highly diverse and highly successful: invasive Australian acacias have not experienced genetic bottlenecks globally

Sara Vicente[1,2,3], Cristina Máguas[2], David M. Richardson[4], Helena Trindade[1], John R. U. Wilson[4,5], Johannes J. Le Roux[3*]

[1]Centro de Estudos do Ambiente e do Mar (CESAM), Faculdade de Ciências da Universidade de Lisboa, Campo Grande 1749-016, Lisboa, Portugal; [2] Centre for Ecology, Evolution and Environmental Changes (cE3c), Faculdade de Ciências da Universidade de Lisboa, Campo Grande 1749-016, Lisboa, Portugal; [3]Department of Biological Sciences, Macquarie University, North Ryde, NSW, Australia; [4]Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Stellenbosch, South Africa; [5]South African National Biodiversity Institute, Kirstenbosch Research Centre, Cape Town, South Africa

**For correspondence. E-mail jaco.leroux@mq.edu.au*

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- **Background and Aims** Invasive species may undergo rapid evolution despite very limited standing genetic diversity. This so-called genetic paradox of biological invasions assumes that an invasive species has experienced (and survived) a genetic bottleneck and then underwent local adaptation in the new range. In this study, we test how often Australian acacias (genus *Acacia*), one of the world's worst invasive tree groups, have experienced genetic bottlenecks and inbreeding.
- **Methods** We collated genetic data from 51 different genetic studies on *Acacia* species to compare genetic diversity between native and invasive populations. These studies analysed 37 different *Acacia* species, with genetic data from the invasive ranges of 11 species, and data from the native range for 36 species (14 of these 36 species are known to be invasive somewhere in the world, and the other 22 are not known to be invasive).
- **Key Results** Levels of genetic diversity are similar in native and invasive populations, and there is little evidence of invasive acacia populations being extensively inbred. Levels of genetic diversity in native range populations also did not differ significantly between species that have and that do not have invasive populations.
- **Conclusion** We attribute our findings to the impressive movement, introduction effort, and human usage of Australian acacias around the world.

Keywords: *Acacia*, admixture, biological invasions, genetic paradox, inbreeding, propagule pressure, rapid evolution, tree invasions, wattles.

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INTRODUCTION

Species introduced by humans to new regions must negotiate a series of barriers before they can achieve substantial population growth and spread over large areas (Blackburn *et al.*, 2011). Understanding the drivers of establishment and invasion success remains a central theme in invasion biology (e.g. Catford *et al.*, 2009; Blackburn *et al.*, 2011). Attributes of the alien species (i.e. invasiveness), their new environments (i.e. invasibility), and how they were introduced (i.e. introduction dynamics) interact to determine invasion success (Pyšek *et al.*, 2020).

Invasive populations frequently stem from multiple introductions of large size of alien propagules (Hufbauer *et al.*, 2013) to areas where climatic conditions are similar to those in the native range (Liu *et al.*, 2020). Many ecological hypotheses have also been formulated around functional traits of alien species, including those related to dispersal, growth and reproduction, to explain invasiveness (Catford *et al*., 2009, Enders *et al*., 2020). Invasion success may not only hinge upon the mean values of these traits, but also their plasticity, especially during the initial phases of invasion, when tolerance of novel environmental conditions will benefit the survival and reproduction of introduced populations (Palacio-López and Gianoli, 2011). Biotic interactions in the introduced range, such as strong release from specialist natural enemies (enemy release hypothesis; Keane and Crawley, 2002) or lack of compatible mutualisms (missed mutualisms hypothesis; Le Roux *et al*., 2020), may further impact invasiveness. Some alien species also have preadapted traits that allow them to survive in certain environments, in what has been termed eco-evolutionary experience (EEE, Saul *et al*., 2013). For instance, alien species that share intermediate levels of EEE with resident natives may prove phenotypically well-matched to their new environments (Petitpierre *et al.*, 2012), but at the same time sufficiently different to overcome possible competition (aka Darwin's naturalisation hypothesis; Catford *et al*., 2019). Importantly, the role of most ecological drivers of invasion success is unrelated to the amount of genetic diversity present in introduced populations.

Its has been suggested that some alien species undergo rapid evolution (within tens to hundreds of generations) to become invasive (e.g. Reznick *et al.*, 2019; van Boheemen *et al.*, 2019).

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Such rapid evolution is intriguing, as invasive populations often suffer strong founder effects and genetic bottlenecks (Dlugosch and Parker, 2008); this has been termed a 'genetic paradox' (Allendorf and Lundquist, 2003) as it seems to contradict the widely held notion that evolutionary responses during invasion is positively correlated with genetic diversity (Estoup *et al.*, 2016). Three conditions must be met for an invasion to be considered a genetic paradox (Estoup *et al.*, 2016). First, the invasive species must experience a genetic bottleneck leading to the loss of genetic variation. Second, bottlenecked populations must survive in the new range without succumbing to problems associated with low genetic variation, like inbreeding depression. Third, the species must adapt to its new environment, i.e. undergo rapid evolution.

Alien species can employ a variety of mechanisms to adapt to their new environments despite low genetic diversity (e.g. Prentis *et al.*, 2008; Li *et al.*, 2019; Cam *et al.*, 2020). For instance, hybridisation between native and invasive species can create novel genotypes (Prentis *et al.*, 2008; Qiao *et al.*, 2019; Mitchell *et al.*, 2019) or epigenetic responses to novel environmental conditions such as DNA methylation can create additional phenotypic variation (e.g. Schrey *et al.*, 2012; Hawes *et al.*, 2019). Native and introduced populations of some species, however, may harbour comparable levels of genetic diversity. In some instances, standing genetic diversity in introduced populations may even exceed levels of diversty in native-range populations, possibly as a result of multiple introductions (e.g. Bossdorf *et al.*, 2005; Cavalcanti *et al.*, 2020), admixture between individuals from different sources (e.g. Genton *et al.*, 2005; van Boheemen *et al.*, 2017), or large introduction sizes (e.g. Roman and Darling, 2007; Kelager *et al.*, 2013).

Studies based on neutral genetic diversity suggest that invasive populations often have lower levels of genetic diversity than their native counterparts (Dlugosch and Parker, 2008). Importantly, however, low neutral genetic diversity may only have a 'mild' effect on the evolutionary capacity of introduced populations, as variation at neutral loci is expected to be more severely impacted by genetic bottlenecks than variation for quantitative traits (Lande 1988). Moreover, unlike quantitative traits, neutral loci are not under selection and, therefore, do not reflect adaptive potential (Reed and Frankham, 2001; Holderegger *et al.*, 2007; Dlugosch *et al.*, 2015). Consequently, variability in

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ecologically-relevant traits can be high in invasive populations, even when neutral genetic diversity is low. Regardless of this, similar levels of neutral genetic diversity in invasive and native populations strongly suggest that the adaptive capacities of invasive populations are likely to be high (Estoup *et al.*, 2016).

Australian acacias are among the world's most problematic invasive plants (Richardson *et al.*, 2011). They have relatively short generation times and reach reproductive maturity within their first few years of growth (often within 2-3 years; Maslin and McDonald, 2004; Gibson *et al.*, 2011), which may facilitate rapid adaptation to their new environments. As fast-growing trees, they have been introduced around the world for numerous purposes such as land reclamation and tannin production (Griffin *et al.*, 2011). At least 25 species are known to be invasive (Richardson *et al.*, 2015; Magona *et al.*, 2018) and are among the most studied taxa in invasion biology, with one area of research that has enjoyed substantial interest over the past decade being the invasion genetics of the group. These genetic studies have provided valuable insights into the invasion histories, dynamics and evolutionary ecology of Australian acacias. For example, Thompson *et al.* (2012, 2015) found some invasive *A. saligna* populations to be genetically diverse, but distinct from native range populations. They found this to be the result of hybridisation and introgression in the native range *prior* to the species' introduction into non-native areas. Other researchers have found reduced genetic diversity to not impede adaptive potential of some invasive acacias (Harris *et al.*, 2012). A common theme in many of these studies is that they compare genetic diversity between native and invasive populations. We took advantage of this unique situation to test how often Australian acacias have experienced genetic bottlenecks (i.e. lower allelic richness, heterozygosity) and higher levels of inbreeding in their invasive populations compared with native populations. We hypothesised that the extensive movement of acacias around the world, associated with frequent human-usage and often accompanied by multiple introductions and genetic admixture, would have led to genetically diverse invasive populations and no genetic bottlenecks.

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MATERIALS AND METHODS

Data collection and analyses

We reviewed literature on population genetic and phylogeographic analyses of Australian acacias in their native and alien ranges. We searched the Web of Science database (https://apps.webofknowledge.com) for publications, using the terms 'population genetic + acacia', 'genetic diversity + acacia', 'phylogenetic + acacia', 'phylogeography + acacia' (searched between 6-9 April 2020). All references listed in retrieved papers were checked for additional resources (i.e., snowball sampling). Publications citing the retrieved papers were also checked (i.e., forward searching). Where possible, we extracted four common population genetic diversity metrics: expected heterozygosity (H_E), observed heterozygosity (H_O), allelic richness (A_r) and inbreeding coefficient (F_{IS}). When not reported, F_{IS} values were calculated as: $(H_E - H_O) / H_E$. We also generated genetic data as part of a microsatellite marker transfer exercise (i.e., cross-amplification of microsatellite markers designed in particular *Acacia* species in other closely related acacias) in our labs for four species in both native and alien populations [Supplementary data– Appendix 1].

Genetic diversity indices were calculated for: a) invasive ranges; b) native ranges for taxa with invasive populations; and c) native ranges for taxa that do not have invasive populations. We treated each country of introduction as a separate data point when studies included individual invasive *Acacia* species from multiple invasive ranges (i.e. countries; e.g. see Thompson *et al.*, 2015). All diversity indices were averaged within each country (if not reported as such) and treated as independent data points in subsequent analyses. We then calculated the proportional change of H_E, H_O and A_r as: [(average value in invasive range – average value in native range) / average value in native range], following Dlugosch and Parker (2008).

Information on the introduction histories of all acacias was compiled from several sources (e.g., Butterfield, 1938; Shaughnessy, 1980; Kull *et al.*, 2008, 2011; Poynton, 2009; Carruthers *et al.*, 2011; Griffin *et al.*, 2011). We were especially interested in the year and purpose of introduction, as

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well as the number of introductions (single or multiple). When a range of years was given for the introduction of a species, the midpoint was taken. We defined seven categories for introduction purpose: agroforestry (e.g. watershed, fodder, shade, etc.); environmental services (e.g. dune stabilisation, erosion control); forestry (e.g. timber, tanbark, etc.); fuelwood/charcoal; horticulture (e.g. cut flower); ornamental; and other (e.g. scientific research). We also searched the literature to identify the age of reproductive maturity for individual species. These data, along with residence times, allowed us to infer the number of generations that acacias might have experienced since introduction.

All statistical analyses were performed in the R statistical environment (R Core Team, 2016). To check for significant shifts in H_E, H_O and A_r in invasive populations, we tested if the calculated mean proportional change of each metric was significantly different from 0 (i.e. no change) by applying the two-tailed Wilcoxon signed test, as the data are not normally distributed ($p < 0.05$ Shapiro-Wilk normality test, and visual inspection of frequency polygons – see Figure 1). For A_r, the one-sample t-test was applied ($p > 0.05$ Shapiro-Wilk normality test). To assess if diversity indices (H_E, H_O, A_r and F_{IS}) differed between ranges, we applied Kruskal-Wallis tests as our data failed the assumptions of normality and homoscedasticity of variances.

RESULTS

In total, 51 studies (including genetic data generated in this study) met our requirements and were included for further analyses: 48 studies were indetified in our search, with an additional two studies identified from their references. Together, these studies analysed 37 different *Acacia* species. Of these, 11 species had invasive range data and 36 species had native range data (14 of these species are known to be invasive somewhere in the world, and the other 22 are not known to be invasive anywhere) (Table 1). We found no significant difference in the sampling intensity (i.e., average number of individuals sampled per population) between these three groups (Kruskal-Wallis, $p > 0.05$; [Supplementary data – Appendix 2]). Eleven studies (i.e., 22% of all studies) estimated genetic

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diversity metrics from newly germinated seedlings, while the remaining studies sampled mature plants in the field [Supplementary data – Appendix 2]. We identified 26 independent introductions (of 10 *Acacia* species) for which data were also available for native range populations to calculate proportional change in H_E and H_O (Figure 1A and 1B, respectively). For A_r, 11 introductions were considered (Figure 1C). The mean proportional change was 0.218 for H_E, 0.286 for H_O, and 0.048 for A_r. Proportional changes revealed an overall significant gain in H_E and H_O in invasive populations ($p < 0.05$ two-tailed Wilcoxon signed rank test, Figure 1A and 1B). Of the 11 invasive *Acacia* species, all had records of being introduced for forestry purposes, while seven had records of introduction for agroforesty and fuelwood/charcoal purposes, six for environmental services, five for ornamental and other purposes, and two for horticulture purposes [Supplementary data – Appendix 2]. In a few instances, the reason for introduction was unknown. The first year of introduction ranged from 1827 to 1971. Seven introductions had unknown introduction dates [Supplementary data – Appendix 2]. We were able to obtain data on both first year of introduction *and* age to first reproduction for 18 introductions (Maslin and McDonald, 2004). From these data we estimated that acacias have, as of 2020, been present in their new ranges between 24–97 generations [Supplementary data – Appendix 2]. Multiple introductions and admixture have been reported in the majority of studies included [Supplementary data – Appendix 2].

In invasive ranges, H_E ranged from 0.248 to 0.720, H_O from 0.230 to 0.780, A_r from 2.097 to 8.454 and F_{IS} from -0.351 to 0.430. In native range populations with invasive conspecifics, H_E ranged from 0.017 to 0.730, H_O from 0.015 to 0.770, A_r from 1.650 to 6.310 and F_{IS} from -0.302 to 0.627. In native range populations with no invasive conspecifics, H_E ranged from 0.109 to 0.834, H_O from 0.078 to 0.871, A_r from 2.140 to 12.043 and F_{IS} from -0.935 to 0.482. We found no significant differences among any of these three groups for any diversity metrics (Figure 2), and no correlation between any of the diversity metrics and residence time (data not shown).

It should be noted that our analyses included data from different molecular marker types that may differ in their sensitivity to genetic bottlenecks. The majority of studies used microsatellite data (n=35), while a few used isozyme (n=13) and dominant fragment markers (n=3) data [Supplementary

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data – Appendix 2]. As all data from the invasive ranges were based on microsatellite analyses, we also compared diversity metrics among the different ranges using microsatellite data only. These results did not differ from those obtained when using the overall dataset, we therefore only report on the latter here.

DISCUSSION

Neutral and adaptive genetic diversity present in invasive populations can be influenced by a number of factors and, therefore, testing the generality of founder events and subsequent genetic bottlenecks would benefit from studies on species, or closely related groups of species, that are invasive in different areas globally, have different introduction histories and human-uses, and thus potentially differ in their levels of genetic diversity. Australian acacias tick many of these boxes (Richardson *et al.*, 2011). By synthesising available genetic data, we add to a growing body of evidence that shows that some invasive species do not experience genetic bottlenecks or extensive inbreeding (e.g. Roman and Darling, 2007; Mohammed *et al.*, 2020). Based on the present analysis, we can also confidently conclude that no genetic paradox exists for any of the Australian acacias we studied and that standing genetic variation is similar in native and invasive populations.

The global success of Australian acacias has been attributed to their extensive usage by humans (Castro-Díez *et al.*, 2011; Richardson *et al.*, 2011). These trees have been widely planted from the mid-19th century onwards, a time that coincides with an increasing global demand for fast-growing trees (Bennett, 2011). Acacias have been purposefully introduced for a variety of reasons, often under circumstances that called for high propagule pressure, i.e., multiple introductions, each often consisting of a high number of individuals (Le Roux *et al.*, 2011; Richardson *et al.*, 2011; Donaldson *et al.*, 2014). This likely explains the similar levels of heterozygosity and inbreeding between some native and invasive acacia populations, or the low inbreeding in some invasive populations, we observed. For example, for the silver wattle, *A. dealbata*, invasive populations had lower inbreeding coefficients (average F_{IS} = -0.13) than native-range populations (average F_{IS} = 0.06).

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For this species, invasive populations were from numerous areas around the world (Hirsch et al. 2019, 2021) and population genetic analyses indicate that the majority of these populations are characterized by high genetic diversity and low levels of genetic structure, likely because they originated from multiple introductions (Hirsch et al. 2011). Similarly, over 280 million seeds of the Port Jackson willow, *A. saligna*, have been imported to South Africa (Le Roux *et al.*, 2011) and were broadcast into the environment for dune stabilisation. These seeds were not only sourced from Australia, but also from secondary ranges such as France (Poynton, 2009). For the black wattle, *A. mearnsii*, millions of seeds were introduced to start forestry plantations for tannin production in South Africa (Le Roux *et al.*, 2011). At least eight independent introductions occurred between 1850-1985, involving seeds collected from throughout the species' native range south-eastern Australia (Poynton, 2009). Most acacias have large native range sizes, offering a variety of sources for introduction to different environmental and climatic conditions (Richardson *et al.*, 2011). We found multiple introductions to be the norm for acacias, often accompanied by admixture between distinct genetic lineages in their new ranges [Supplementary data – Appendix 2]. This probably explains the overall increase in heterozygosity, and concurrent decrease in inbreeding, observed in invasive populations (Dlugosh and Parker, 2008).

Our finding that invasive Australian acacias experienced no genetic bottlenecks, together with a lack of marker-based evidence for inbreeding, has important implications. First, high genetic diversity increases the likelihood for introducing phenotypes well-matched to new environmental conditions, i.e. of introducing pre-adapted phenotypes (e.g. Duncan and Williams, 2002; Bossdorf *et al.*, 2008). Second, multiple introductions from distinct sources create opportunities for genetic admixture which may provide novel phenotypic variation to fuel rapid evolution (e.g. Lavergne and Molofsky, 2007; Xia *et al.*, 2020). Even without genetic admixture, high genetic diversity is expected to accelerate microevolution via both neutral (e.g. spatial sorting; Berthouly-Salazar *et al.*, 2012) and deterministic (i.e. natural selection; Banerjee *et al.*, 2019) processes.

High genetic diversity at neutral markers likely translates into high adaptive diversity (Caballero and García-Dorado, 2013; Vilas *et al.*, 2015). While none of the benefits of high genetic

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diversity described above have been explicitly tested in invasive acacias anywhere in the world, our analyses clearly illustrate that all these options are available to most invasive acacias. Many invasive acacias have been introduced long ago (up to 97 generations for the species included here), providing ample time for rapid evolution to have occurred (*sensu* Reznick *et al.*, 2019) Future research should include assessing whether genetically-diverse invasive acacias have undergone rapid evolution in their alien ranges.

Taken together, we show how humans have profoundly shaped the worldwide invasion of Australian acacias, characterised by multiple introductions of large size and admixture, leading to genetically-diverse populations with high adaptive capacities. While these findings may not be applicable to invasive species in general, they do provide novel insights into the invasion dynamics of one of the world's most successful invasive plant groups.

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Figure Captions

Figure 1: The proportional change of (A) expected heterozygosity, (B) observed heterozygosity, and (C) allelic richness in invasive populations of acacias relative to their native counterparts. An 'independent comparison' is considered as the comparision of the diversity metrics of the same species of *Acacia* between an invaded range and the native range. Different countries of introduction were considered as different invaded ranges. Rugs represent the distribution of purposes of introduction. Detailed information can be found in Supplementary Information – Appendix 2. *$p \leqslant 0.05$, two-tailed Wilcoxon signed rank test.

Figure 2: Box plots showing (A) expected heterozygosity, (B) observed heterozygosity, (C) inbreeding coefficient and (D) allelic richness by range type (native range for taxa that do not have invasive populations; native range for taxa with invasive populations; and invasive ranges). Kruskal-Wallis tests show no significant differences among ranges for any of the considered metrics.

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Table

Table 1: Diversity metrics extracted from 51 studies on molecular variation of Australian *Acacia* species. H_E – Expected heterozygosity; H_O – Observed heterozygosity; A_r – Allelic richness; F_{IS} – Inbreeding coefficient. A) Data for different populations; B) Mean and standard deviation of the diversity metrics with data grouped according to range type (invasive range; native range for taxa with invasive ranges, marked as native*; native range for taxa with no invasive ranges)

1A

Range	Species	H_E	H_O	A_r	F_{IS}	Reference
Invasive	*A. auriculiformis*	0.422	0.570	-	-0.351	Adamski et al. 2013
Invasive	*A. cincinnata*	0.451	0.481	-	-0.066	Adamski et al. 2013
Invasive	*A. crassicarpa*	0.455	0.486	-	-0.070	Adamski et al. 2013
Invasive	*A. dealbata*	0.330	0.408	2.097	-0.206	Hirsch et al. 2021
Invasive	*A. dealbata*	0.473	0.555	2.815	-0.164	Hirsch et al. 2021
Invasive	*A. dealbata*	0.432	0.475	2.864	-0.088	Hirsch et al. 2021
Invasive	*A. dealbata*	0.471	0.522	2.895	-0.067	Hirsch et al. 2021
Invasive	*A. dealbata*	0.445	0.448	2.898	-0.012	Hirsch et al. 2021
Invasive	*A. dealbata*	0.433	0.552	2.731	-0.266	Hirsch et al. 2021
Invasive	*A. dealbata*	0.403	0.459	2.413	-0.114	Hirsch et al. 2019
Invasive	*A. longifolia*	0.720	0.740	6.060	-0.031	Vicente et al. (this study)

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1A

Range	Species	H_E	H_O	A_r	F_{IS}	Reference
Invasive	*A. longifolia*	0.500	0.515	-	-0.039	Vicente et al. 2018
Invasive	*A. mangium*	0.248	0.230	-	0.073	Adamski et al. 2013
Invasive	*A. mangium*	0.623	0.502	8.454	0.169	Yuskianti & Isoda 2012
Invasive	*A. mangium*	0.707	0.604	-	0.145	Butcher et al. 2004
Invasive	*A. mearnsii*	0.550	0.430	7.080	0.250	Bairu et al. 2019
Invasive	*A. melanoxylon*	0.433	0.457	-	-0.056	Adamski et al. 2013
Invasive	*A. melanoxylon*	0.710	0.780	5.540	-0.098	Vicente et al. (this study)
Invasive	*A. podalyriifolia*	0.630	0.630	4.130	0.002	Vicente et al. (this study)
Invasive	*A. pycnantha*	0.600	0.650	-	-0.066	Le Roux et al. 2013
Invasive	*A. pycnantha*	0.590	0.740	5.040	-0.257	Vicente et al. (this study)
Invasive	*A. saligna*	0.435	0.360	-	0.088	Thompson et al. 2015
Invasive	*A. saligna*	0.530	0.390	-	0.230	Thompson et al. 2015
Invasive	*A. saligna*	0.640	0.360	-	0.430	Thompson et al. 2015
Invasive	*A. saligna*	0.640	0.470	-	0.290	Thompson et al. 2015
Invasive	*A. saligna*	0.435	0.332	-	0.238	Thompson et al. 2012
Invasive	*A. saligna*	0.406	0.442	-	-0.081	Millar & Byrne 2012
Native*	*A. ancistrocarpa*	0.525	0.426	5.400	0.188	Levy et al. 2016
Native*	*A. auriculiformis*	0.081	0.071	-	0.123	Wickneswari & Norwati 1993
Native*	*A. auriculiformis*	0.600	0.500	-	0.180	Le et al. 2016
Native*	*A. crassicarpa*	0.222	0.083	-	0.627	Shukor & Chubo 2003
Native*	*A. crassicarpa*	0.630	0.600	-	0.050	McKinnon et al. 2018
Native*	*A. cyclops*	0.269	0.352	1.823	-0.221	Millar et al. 2019

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1A

Range	Species	H_E	H_O	A_r	F_{IS}	Reference
Native*	*A. dealbata*	0.110	0.100	1.650	0.134	Broadhurst et al. 2008
Native*	*A. dealbata*	0.549	0.481	-	0.124	Guillemaud et al. 2015
Native*	*A. dealbata*	0.460	0.495	3.375	-0.076	Hirsch et al. 2018
Native*	*A. longifolia*	0.730	0.760	6.230	-0.053	Vicente et al. (this study)
Native*	*A. mangium*	0.131	0.124	-	0.058	Butcher et al. 1998
Native*	*A. mangium*	0.017	0.015	-	0.118	Moran et al. 1989
Native*	*A. mangium*	0.560	0.450	-	0.200	Le et al. 2016
Native*	*A. mangium*	0.692	0.640	-	0.075	Butcher et al. 2004
Native*	*A. mearnsii*	0.179	0.164	-	0.057	Searle et al. 2000
Native*	*A. melanoxylon*	0.208	0.177	-	0.113	Playford et al. 1993
Native*	*A. melanoxylon*	0.720	0.650	6.310	0.103	Vicente et al. (this study)
Native*	*A. microbotrya*	0.370	0.364	2.220	-0.016	Binks et al. 2015
Native*	*A. microbotrya*	0.172	0.123	-	0.151	Elliot et al. 2002
Native*	*A. podalyriifolia*	0.590	0.770	3.400	-0.302	Vicente et al. (this study)
Native*	*A. pycnantha*	0.580	0.670	-	-0.133	Le Roux et al. 2013
Native*	*A. pycnantha*	0.590	0.660	4.950	-0.121	Vicente et al. (this study)
Native*	*A. saligna*	0.455	0.335	-	0.265	Thompson et al. 2015
Native*	*A. saligna*	0.505	0.417	-	0.174	Thompson et al. 2012
Native*	*A. saligna*	0.561	0.461	-	0.170	Millar & Byrne 2012
Native*	*A. saligna*	0.498	0.456	-	0.089	Millar et al. 2011
Native*	*A. saligna*	0.476	0.427	-	0.107	Millar et al. 2008
Native*	*A. saligna*	0.282	0.278	-	0.030	George et al. 2006

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1A

Range	Species	H_E	H_O	A_r	F_{IS}	Reference
Native*	*A. saligna*	0.526	0.391	-	0.257	Millar & Byrne 2007
Native*	*A. tumida*	0.149	0.133	-	0.111	McDonald et al. 2003
Native	*A. acuminata*	0.263	0.154	-	0.299	Broadhurst & Coates 2002
Native	*A. adinophylla*	0.613	0.871	-	-0.420	Nevill & Wardell-Johnson 2016
Native	*A. amblyophylla*	0.428	0.433	2.340	-0.053	Binks et al. 2015
Native	*A. anfractuosa*	0.380	0.200	-	0.380	Coates et al. 2006
Native	*A. anomala*	0.144	0.164	-	-0.135	Coates 1988
Native	*A. atkinsiana*	0.426	0.430	3.000	-0.029	Levy et al. 2016
Native	*A. atkinsiana*	0.493	0.534	-	-0.084	Levy et al. 2014
Native	*A. attenuata*	0.239	0.125	-	0.482	Brownlie et al. 2009
Native	*A. aulacocarpa*	0.112	0.104	-	0.084	McGranahan et al. 1997
Native	*A. carneorum*	0.245	0.473	-	-0.935	Roberts et al. 2013
Native	*A. carneorum*	-	0.540	-	-	Roberts et al. 2017
Native	*A. daphnifolia*	0.397	0.390	2.320	0.021	Binks et al. 2015
Native	*A. harpophylla*	0.834	0.732	12.043	0.111	Lepais & Bacles 2011
Native	*A. karina*	0.779	0.704	-	0.096	Nevill et al. 2010
Native	*A. karina*	0.735	0.705	6.400	0.037	Funnekotter et al. 2019
Native	*A. ligulata*	0.750	-	-	0.380	Forrest et al. 2015
Native	*A. loderi*	0.560	0.498	3.200	-0.096	Roberts et al. 2016
Native	*A. loderi*	0.472	0.432	-	0.085	Roberts et al. 2013
Native	*A. melvillei*	0.700	-	-	0.380	Forrest et al. 2015
Native	*A. montana*	0.677	0.540	-	0.202	Hopley et al. 2015

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1A

Range	Species	H_E	H_O	A_r	F_{IS}	Reference
Native	*A. oldfieldii*	0.168	0.078	-	0.332	Broadhurst & Coates 2002
Native	*A. pendula*	0.738	-	-	0.214	Forrest et al. 2015
Native	*A. sciophanes*	0.300	0.180	-	0.360	Coates et al. 2006
Native	*A. splendens*	0.338	0.322	2.140	0.000	Binks et al. 2015
Native	*A. splendens*	0.109	0.094	-	0.035	Elliot et al. 2002
Native	*A. stenophylla*	0.439	0.368	-	0.173	Murray et al. 2019
Native	*A. stenophylla*	0.432	0.354	-	0.108	Murray et al. 2018
Native	*A. woodmaniorum*	0.531	0.529	2.730	-0.008	Millar et al. 2013
Native	*A. woodmaniorum*	0.559	0.511	-	0.084	Millar 2009

1B

Range	*n*	H_E	H_O	A_r	F_{IS}
Invasive	27	0.508 ± 0.120	0.503 ± 0.129	4.232 ± 2.025	-0.004 ± 0.185
Native*	30	0.451 ± 0.211	0.386 ± 0.220	3.929 ± 1.848	0.086 ± 0.167
Native	29	0.459 ± 0.215	0.402 ± 0.219	4.272 ± 3.426	0.075 ± 0.279

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Figure 1

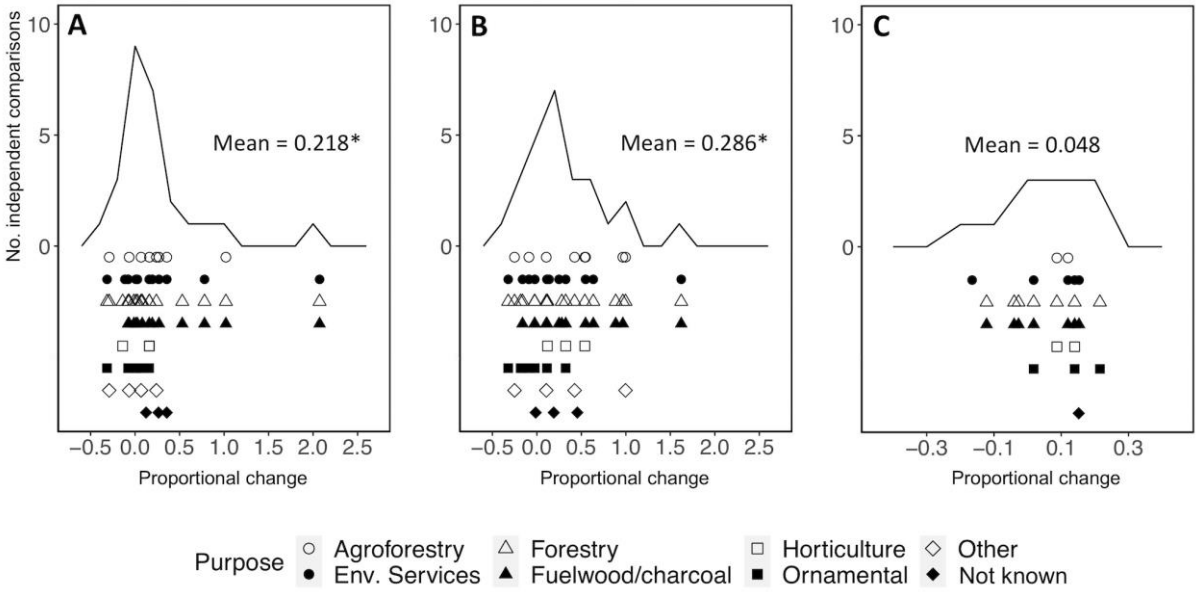

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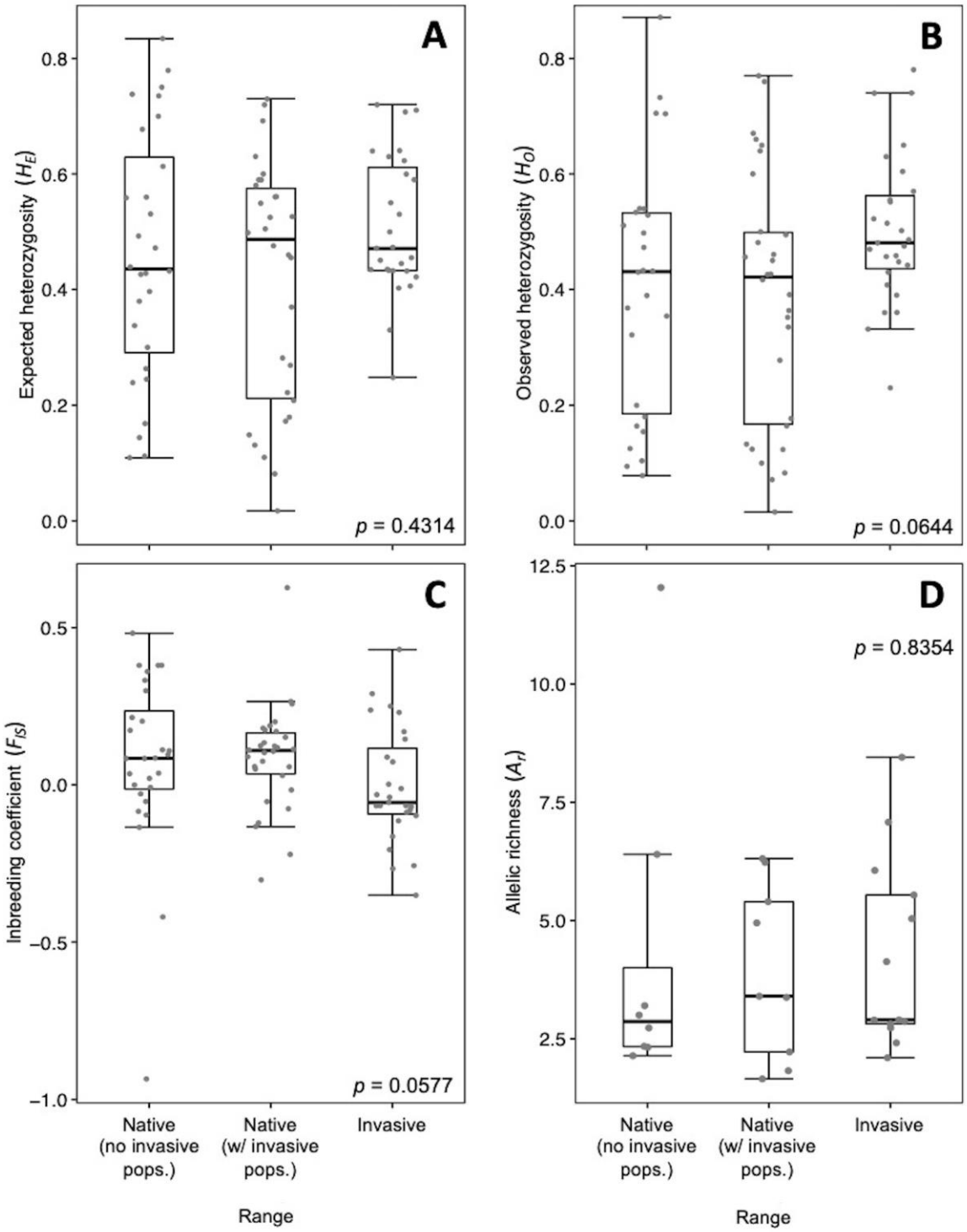
Figure 2



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